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Evaluation of Models that Predict Mortality and Topkill caused by Douglas-fir Tussock Moth

Evaluation of models that predict mortality and topkill caused by Douglas-fir tussock moth

Katharine A. Sheehan[1], Lance R. David[2], Boyd E. Wickman[3], Elizabeth A. Willhite[1], John M. Wenz[4], Julie C. Weatherby[5], Eric L. Smith[6], Richard R. Mason[7], Bruce B. Hostetler[1], and Tommy F. Gregg[1]

Background

During the mid-1970s outbreak of Douglas-fir tussock moth (DFTM) in the Blue Mountains of northeastern Oregon, Boyd Wickman recorded initial stand conditions, defoliation patterns, and subsequent tree mortality and topkill (Wickman 1978). Wickman's observations offer a rare opportunity to test the damage predictions made by the Forest Vegetation Simulator (FVS, previously known as the Stand Prognosis model) using a variety of options for simulating DFTM effects. Both the DFTM outbreak model (Monserud and Crookston 1982) and the western spruce budworm (WSB) damage model (Crookston et al. 1990) were used to simulate the effects of defoliation by tussock moth.

Wickman has reported the effects of defoliation by DFTM on both tree mortality and topkill (Wickman 1978) and growth loss (Wickman et al. 1980). In these analyses, damage was described for individual trees (by tree species); that is, all sample trees of the same species were pooled together. We chose to treat the 29 subareas as stands (and plots as subsamples of those stands) so that we could test the ability of various FVS/DFTM outbreak model and FVS/WSB damage model options to predict damage caused by DFTM defoliation.

Both the DFTM outbreak model and the WSB damage model were evaluated. To use the damage model, we translated the **total tree defoliation** estimates recorded by Wickman (1979) into estimates of **missing biomass** as described in Sheehan et al. (1994). We examined the effects of defoliation on tree mortality, topkill rate, and topkill length.

1 Forest Pest Management, Pacific Northwest Region, USDA-Forest Service, Portland, OR.
2 Management Assistance Corporation of America, Portland, OR.
3 Pacific Northwest Research Station, USDA-Forest Service, Bend, OR.
4 Forest Pest Management, Pacific Southwest Region, USDA-Forest Service, Sonora, CA.
5 Forest Pest Management, Intermountain Region, USDA-Forest Service, Boise, ID.
6 Forest Pest Management, Methods Application Group, USDA-Forest Service, Fort Collins, CO.
7 Pacific Northwest Research Station, USDA-Forest Service, LaGrande, OR.

Objective

Compare the amounts of tree mortality and topkill predicted by FVS with the DFTM outbreak model or the WSB damage model using a range of options for simulating DFTM effects with the actual damage observed by Wickman during the mid-1970's Blue Mountains outbreak.

Methods

Observed effects -- Wickman's damage observations have previously been described (Wickman 1978). A total of 29 subareas were sampled, with an average of 11.8 plots per subarea and 8.5 trees per plot. Circular 1/50th-acre plots were used, and all trees over 1 inch in diameter at breast height were measured. A total of 2,918 trees were sampled, and the tree species included grand fir (77%), Douglas-fir (15%), western larch (4%), Engelmann spruce (2%), subalpine fir (1%), and other species (1%, consisting of lodgepole pine, ponderosa pine, and unidentified species).

Total tree defoliation was measured for each tree during two consecutive years (generally 1972 and 1973), and mortality was recorded annually from 1972 through 1976. The extent of topkill was also noted when present. See the appendix for further details about this data set.

Predicted effects -- Six different model options were simulated for each observed subarea:

(1) ***No defoliation*** *-- To provide an estimate of background mortality and topkill, one simulation featured the base FVS model with no defoliation. When we tried to use the WSB damage model with keywords that specified no defoliation, FVS would bypass the damage model. Providing extremely low defoliation values (0.01 percent defoliation for all host foliage) had virtually no effect on damage predictions.*

(2) ***DFTM outbreak model*** *-- One simulation used the DFTM outbreak model by scheduling an outbreak to start in 1972. No changes were made to the default parameter values.*

(3) ***WSB damage model / rules-of-thumb*** *-- The general "rules-of-thumb" that are shown in Table 1 were used to translate total tree defoliation observations into missing biomass estimates. The WSB damage model was then used to simulate the effects of those missing biomass estimates.*

(4) ***WSB damage model / unadjusted estimates*** *-- Based on field observations made in 1991 and 1992, two methods for describing the relation between total tree defoliation and missing biomass (by crown third and foliage age) were described (Sheehan et al. 1994). One method results in "unadjusted estimates" of missing biomass that range from 5% to 95%. These unadjusted estimates were then used with the WSB damage model to simulate the effects of defoliation.*

(5) ***WSB damage model / adjusted estimates*** -- *The other method described by Sheehan et al. (1994) results in missing biomass estimates that are adjusted so that they range from 0 to 99.9%.*

(6) ***WSB damage model / extremely heavy*** -- *As a point of reference, the final set of keywords that was used with the damage model represented extremely heavy defoliation. For this scenario, missing biomass was set to 98.5% for all host foliage.*

The Blue Mountains variant of the FVS version 6.2 with either the WSB damage model or the DFTM outbreak model attached was used for all simulations. Each simulation started in 1972 and ran for 3 cycles with the cycle length set to 5 years. The WSB and DFTM models were active during the first cycle only, and predicted tree mortality and topkill was summarized in the fifth year after the start of the outbreak. Damage predicted by the WSB damage model was reported using the STATDATA keyword and an external program was used to summarize the results by size class. The DFTM model results were summarized by an external program from the DFTM "SUMMARY OF TREE CLASS CHARACTERISTICS" table that follows the FVS summaries and tables in the standard FVS output file.

Results

Tree mortality -- Figures 1 through 6 summarize the relation between tree mortality and two different measures of defoliation. First, the relation between maximum defoliation (defined as the highest percent defoliation observed, which may occur in either year 1 or year 2) and tree mortality rate is shown separately for the two main hosts and the three size classes. Tree mortality rate includes mortality attributed to either DFTM or bark beetles for the observations and to all mortality sources for the model simulations; logging is the main mortality source that was excluded from the tree mortality rate for observations (see appendix), while the FVS output does not display mortality by cause of death. Subareas with less than four trees in a given tree species and size class category were excluded.

*We examined the fit of three equations to each of the six sets of observations (2 species, 3 size classes): linear (Y=B*X+A), log (Y=B*Ln(X)+A), and exponential (Ln(Y)=B*X+A). For the observations, the linear models fit best in all but one case, with* R^2 *values ranging from .55 to .81; for the one exception (large Douglas-firs), the fit of the linear equation was within 6% of the fit of the exponential equation. For all six models (including no defoliation), both linear and log equations were fit to the predicted rates, and in each case the log equation either gave the best fit or was nearly equal to the linear equation. The fit was very poor for all models, and ranged from .00 to .29.*

We also examined the relation between cumulative defoliation (defined as observed percent defoliation in year 1 plus observed percent defoliation in year 2; theoretical range = 1 to 200) and tree mortality rate. Use of cumulative defoliation in place of maximum defolation gave much better fits for the models (excluding no defoliation; R^2 *values ranged from .28 to .51) and much poorer fits for the observations (.27 to .56).*

<u>Topkill rate</u> -- The relation between maximum defoliation and topkill rate is shown in figures 7 to 12. Topkill rate is the proportion of the initial number of trees present that were observed (or predicted) to have dead tops after 5 years. The models tended to underestimate the observed topkill rate except when defoliation is low and/or for large Douglas-firs. The relation between defoliation and topkill rate was weak for the observations (R^2 values ranged from .01 to .30 when fit to log equations and .00 to .41 when fit to linear equations) and virtually non-existant for the six models with one exception. Most R^2 values for the model predictions were less than .10 except for small Douglas-firs, where the R^2 values for the three non-extreme damage models ranged from .58 to .73 when fit to log equations. Similar results were found when cumulative defoliation and topkill rates were examined.

<u>Topkill extent</u> -- The average extent of topkill (average length of dead top in topkilled trees) is plotted against maximum defoliation in figures 13 to 18. In most cases, the relation between defoliation and topkill extent was very weak (R^2 values were usually less than .20 when fit to a log equation for both observations and predictions) and the observed amount of topkill was equal to or greater than the predicted amounts of topkill. For large and (to a lesser degree) medium Douglas-firs, however, the models overpredicted topkill extent.

<u>Discussion</u>

<u>Tree mortality</u> -- Although there was tremendous variability in the relative ability of the different models to simulate the observed mortality rates, a few general trends can be discerned from figures 1-6:

* *The three non-extreme WSB damage model simulations (rules-of-thumb, adjusted, and unadjusted) gave very similar results, and probably could be used interchangeably.*

* *The WSB damage models generally overestimated mortality in small trees; for medium and large trees, the damage model mortality predictions were relatively close to the observed mortality rates for grand fir and much lower than observed for Douglas-fir.*

* *Predictions made by the DFTM outbreak model generally matched the predictions made by the WSB damage models under the maximum defoliation scenario.*

* *Mortality rates predicted by the DFTM outbreak model were generally much higher than observed for grand fir. For Douglas-fir, however, the mortality rates were generally higher than observed in lightly defoliated stands but lower than observed in heavily defoliated stands.*

When maximum defoliation was used to predict mortality rates, we obtained relatively good fits for the observations and poor fits for the models. When cumulative defoliation was used, we obtained much poorer fits for the observed data and much better fits for the three non-extreme WSB models (rules-of-thumb, adjusted, and unadjusted). Cumulative defoliation is a poor measure for summarizing two years of total tree defolation because it may double-count defoliation; for example, when trees are heavily defoliated for 2 years in a

row, much of the defoliation observed in the second year may have occurred in the first year. On the other hand, when maximum defoliation is used, a tree that has 75% total tree defoliation in one year and 80% defoliation during the following year is given the same maximum defoliation rating as a tree that has 10% defoliation in year 1 and 80% defoliation in year 2; the cumulative defoliation estimate, however, would be different for those two trees. Thus, maximum defoliation is a better summary for two years of total tree defoliation estimates, while cumulative defoliation is a better summary of two years of missing biomass estimates.

When Wickman (1978) analyzed these data by species (all stands combined), he found that mortality rates were low except at the highest total tree defoliation levels (figure 19). We found similar results when either average missing biomass or maximum missing biomass was evaluated (figure 19, table 2). These data indicate that at the heaviest defoliation levels, small changes in estimated defoliation may lead to large changes in predicted mortality.

When the DFTM outbreak model was tested against Wickman's data, the two main sources of error are (1) predicting mid-crown branch defoliation and (2) converting branch defoliation to whole-tree defoliation. The translation of defoliation into tree mortality was probably not a source of error because the DFTM model uses mortality rates that are virtually identical to those observed by Wickman (Monserud and Crookston 1982, Colbert and Campbell 1978; shown in table 2). The branch defoliation to whole-tree defoliation conversion process has already been shown to be very sensitive to minor changes at certain defoliation levels (Monserud and Crookston 1982, Gillespie et al. 1990[1]; see figure 20).

When the WSB damage model was tested against Wickman's data, the two main sources of error are (1) converting Wickman's total tree defoliation estimates into missing biomass estimates and (2) predicting tree mortality based on cumulative missing biomass, tree diameter, and relative basal area. The former source is addressed in Sheehan et al. (1994), and table 3 summarizes the missing biomass estimates by initial total tree defoliation category.

The latter source is probably much more significant. Defoliation by western spruce budworm in a given area usually increases more gradually from year to year relative to defoliation by DFTM; defoliation often decreases at a slower rate, too. The mortality models developed by Crookston (1991; see figure 21) for the WSB damage model were designed to simulate the budworm defoliation pattern, and therefore use cumulative defoliation over a five-year period to summarize the defoliation history of a tree. When cumulative defoliation is 200%, for example, mortality rates are low unless the relative basal area is very high or the tree is very small (figure 21) -- which is reasonable if the actual defoliation averaged 40% over a 5-year period (as might be expected for budworm) but not if there was virtually no defoliation for 3 years followed by extremely heavy defoliation for 2 years (as might be expected for DFTM).

[1] Gillespie, Andrew J.R.; David, Lance; Thompson, Matt. Preliminary report on attempts to modify the branch-tree defoliation relationship of the Douglas-fir tussock moth model. Unpublished report, 18 pages, June 1990.

Wickman (1978) showed that even one year of very heavy defoliation has a high probability of causing mortality regardless of tree diameter or stand conditions.

Topkill rate -- The models tended to underestimate topkill rate except when defoliation is low and/or for large Douglas-firs. For the observations, topkill rate generally increased as defoliation increased, although the relation is weak. The six models showed virtually no relation to defoliation, except in the case of small Douglas-firs, where topkill rate decreased with increasing defoliation and the relation was relatively strong. Topkill rates may be affected by the concurrent mortality rates because if those mortality rates are high, then few trees survive to be available for topkilling. As with mortality rates, the three non-extreme WSB damage model options gave nearly identical results, and could probably be used interchangeably.

Topkill extent -- For Douglas-firs, the models generally overestimated the extent of topkill, while no trend is apparent for grand firs. For both observations and predictions, the relation between defoliation and topkill extent is extremely weak. In a few cases, topkill extent appeared to decrease with increasing defoliation; this effect may be due to a relatively small sample size and/or to sampling error. Additional error was probably introduced when we translated Wickman's topkill codes into amounts (in feet) topkilled per tree (as described in note 6 of the appendix).

Conclusions

(1) The three WSB damage model options for translating total tree defoliation into missing biomass gave similar results and could be used interchangeably. Of those three options (rules-of-thumb, unadjusted estimates, and adjusted estimates), the rules-of-thumb (shown in table 1) were much simpler and easier to apply than the other two.

(2) In most cases, both the WSB damage model and the DFTM outbreak model performed poorly. For the WSB damage model, the most important source of error was our attempt to apply tree mortality equations that were developed for budworm to DFTM; those mortality equations usually underestimated the effects of short episodes of severe defoliation that are so typical of DFTM outbreaks. For the DFTM outbreak model, the translation of mid-crown branch defoliation to whole-tree defoliation was probably the weakest link.

(3) To more accurately incorporate the effects of DFTM on FVS (formerly Prognosis) predictions, a DFTM damage model should be developed. This new damage model would use defoliation patterns supplied by the user (as is the case for the WSB damage model) and would lookup the corresponding tree effects (mortality, topkill, and growth loss) in tables based on the publications of Wickman (1978, 1980). Users should be allowed to specify defoliation in terms of either total tree defoliation or missing biomass.

Acknowledgments

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*Table 1. Rules-of-thumb for translating **total tree defolation** into **missing biomass**, developed by K.Sheehan based on theoretical foliage distribution.*

total tree defoliation	missing biomass					
	top		middle		bottom	
	new	old	new	old	new	old
0%	0%	0%	0%	0%	0%	0%
10	100	30	90	15	80	10
25	100	90	100	30	100	20
50	100	100	100	60	100	40
75	100	100	100	100	100	70
90	100	100	100	100	100	85
99	100	100	100	100	100	95
100	100	100	100	100	100	100

Table 2. Observed grand fir mortality rates caused by DFTM and bark beetles summarized for three measures of defoliation (n=2245), and the corresponding rates used in the DFTM outbreak model (source: Colbert and Campbell 1978, table 11-2).

defol. category midpoint	Maximum[1] Total tree defol. percent mortality caused by: DFTM	beetles	Average[2] missing biomass percent mortality caused by: DFTM	beetles	Maximum missing biomass percent mortality caused by: DFTM	beetles	rate used in DFTM model DFTM
0	4.2	20.8	4.2	20.8	4.2	20.8	0.0
10	0	.2	0	0	0	0	0
25	0	.8	.2	.7	0	.8	0
50	0.6	1.1	2.4	1.4	.2	.5	.9
75	3.4	3.4	9.4	2.0	.5	1.1	2.8
90	16.2	7.9	25.0	10.4	14.3	2.9	17.3
99	48.3	5.0	74.1	6.9	27.3	17.2	47.7[3]
100	93.8	1.7	100.0	0	93.9	1.7	92.3

1 Total tree defoliation (TTD) was recorded for each tree for two consecutive years. Maximum TTD represents the highest value recorded for a tree (either year 1 or year 2).

2 For each tree, the two years of TTD estimates were translated into whole-tree missing biomass (MB) estimates by first converting each TTD estimate into six MB estimates per tree (new and old foliage for each crown third) using the rules-of thumb shown in table 1. The six MB estimates per tree were weighted according to the distribution of foliage among crown thirds and foliage age classes reported by Crookston (1991, tables 7 and 9), resulting in one whole-tree MB estimate for each TTD estimate. Calculations were done separately for small, medium, and large trees. Both the average whole-tree MB estimates for the two years and the maximum whole-tree MB estimate are summarized in this table.

3 range of defoliation category = 95 - 99.5%

Table 3. Observed average missing biomass estimates (and standard deviations) summarized by maximum total tree defoliation estimate for grand firs (n=2245).

Maximum total tree defoliation category	Average missing biomass mean	Average missing biomass s.d.	Maximum missing biomass mean	Maximum missing biomass s.d.
0	0.0	0.0	0.0	0.0
10	31.0	10.2	39.3	3.2
25	37.8	10.3	47.9	.5
50	51.2	12.8	63.9	2.3
75	66.6	15.0	85.2	4.6
90	74.1	17.4	90.1	4.0
99	72.4	18.6	93.0	3.3
100	91.4	16.7	100.0	.0

Note regarding Figures 1-18

Figures 1-18 show observations and predictions for 3 dependent variables: tree mortality rate (Figs. 1-6), topkill rate (Figs. 7-12), and topkill length (Figs. 13-18). For each dependent variable, separate graphs are presented for each combination of tree species (grand fir and Douglas-fir) and tree size class (small = <7m, medium = 7-14m, large = >14m). The independent variable is maximum defoliation (the highest percent defoliation recorded during the two years of observations) in all figures. Only those stands with more than three trees in a given tree species/tree size category are included.

*In each figure, each stand (=study areas of Wickman [1978]) is represented by one observation (a solid circle) and the predictions of six different model options (see legend at the top right corner of each page; the six model options are described on pages 2-3). The six predictions associated with each observation are all plotted using the observed maximum defoliation value, even though different defoliation values may have been used by the models. For example, the "no defoliation" model option represents the background mortality predicted by FVS for a given stand when no defoliation occurs. Each figure also shows the fitted log equations (Y=B*ln(X)+A) for the observations and the six model options.*

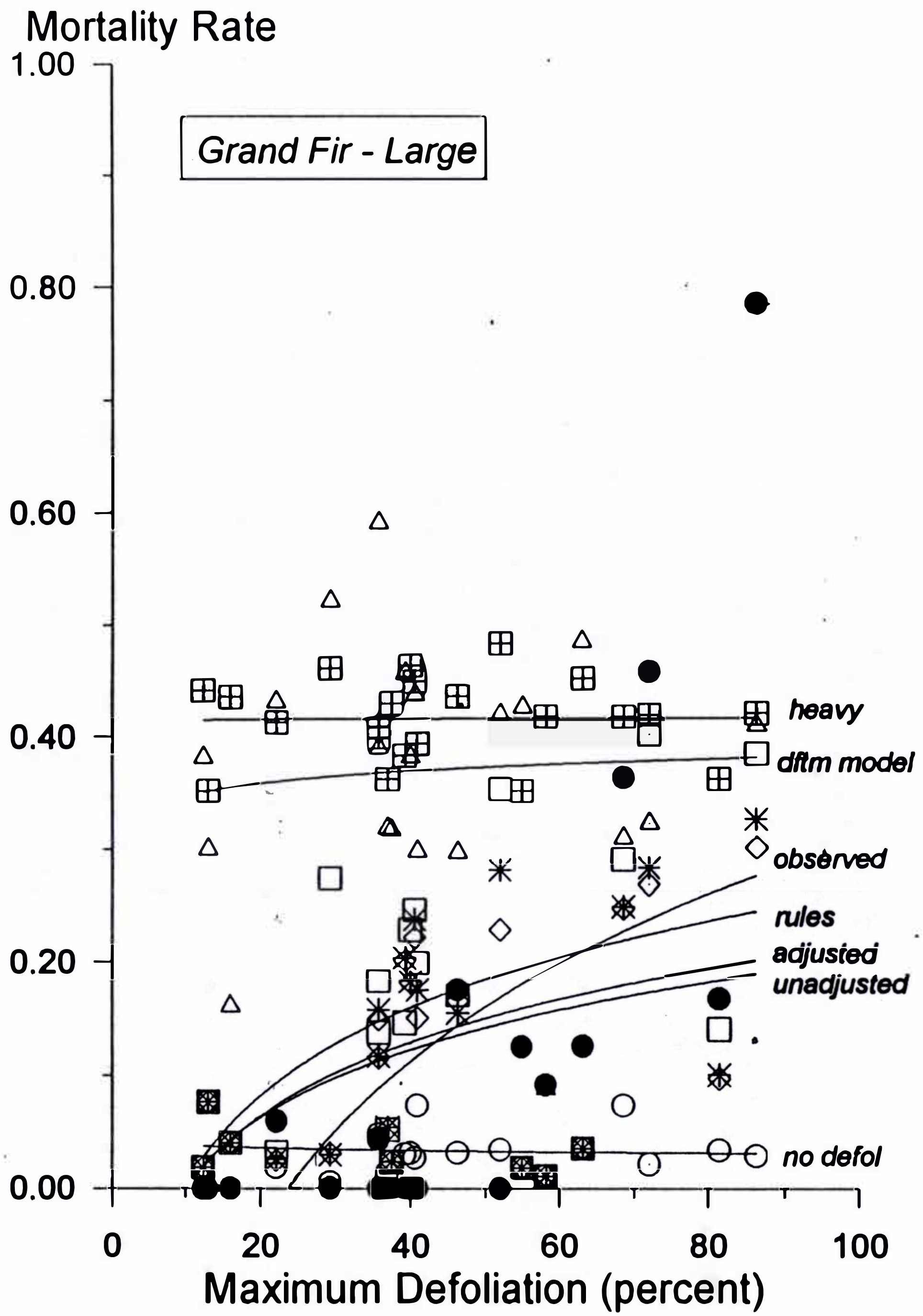

Figure 1 - Relation between mortality rate and defoliation for large grand firs.

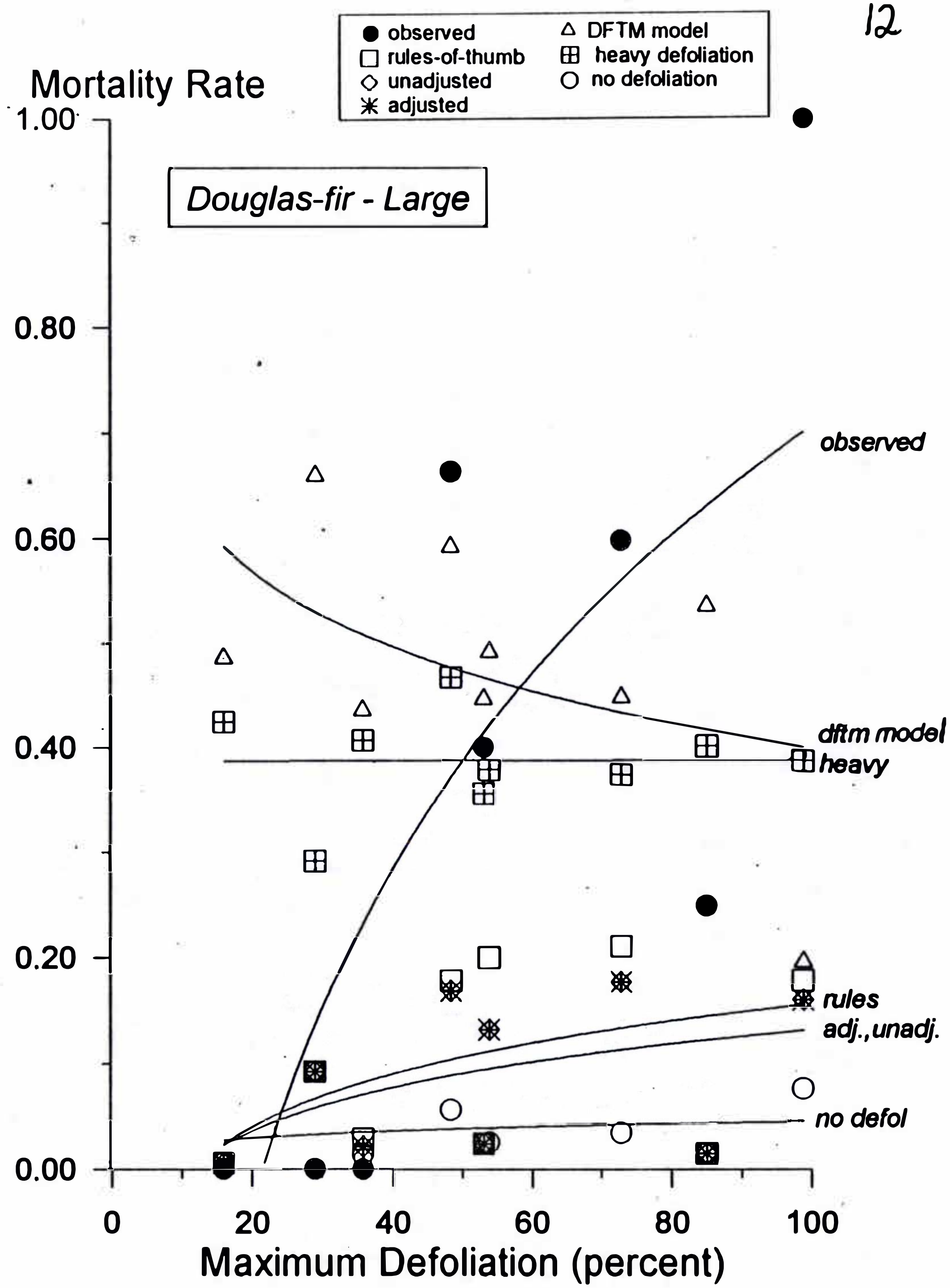

Figure 2 - Relation between mortality rate and defoliation for large Douglas-firs.

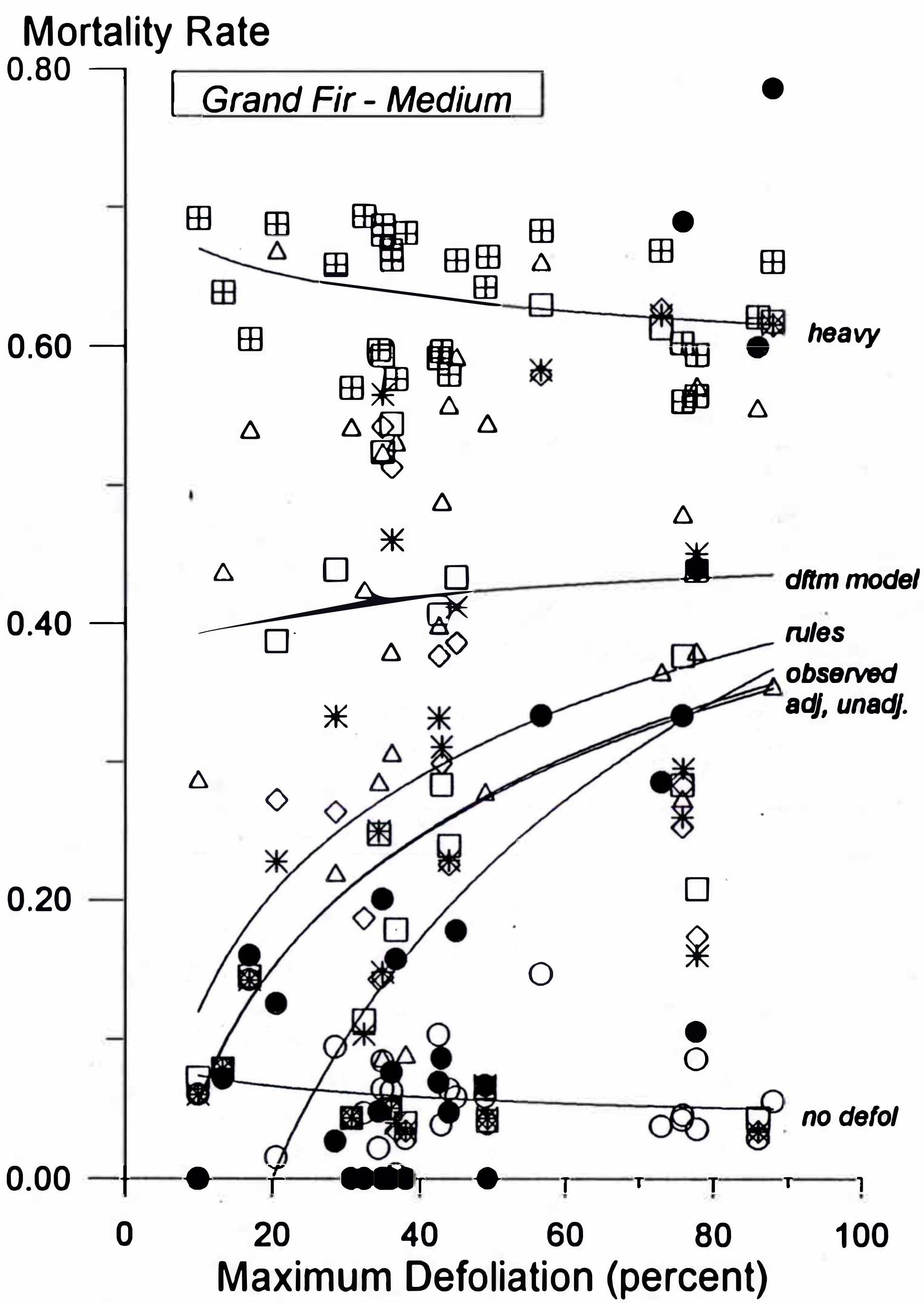

Figure 3 - Relation between mortality rate and defoliation for medium grand firs.

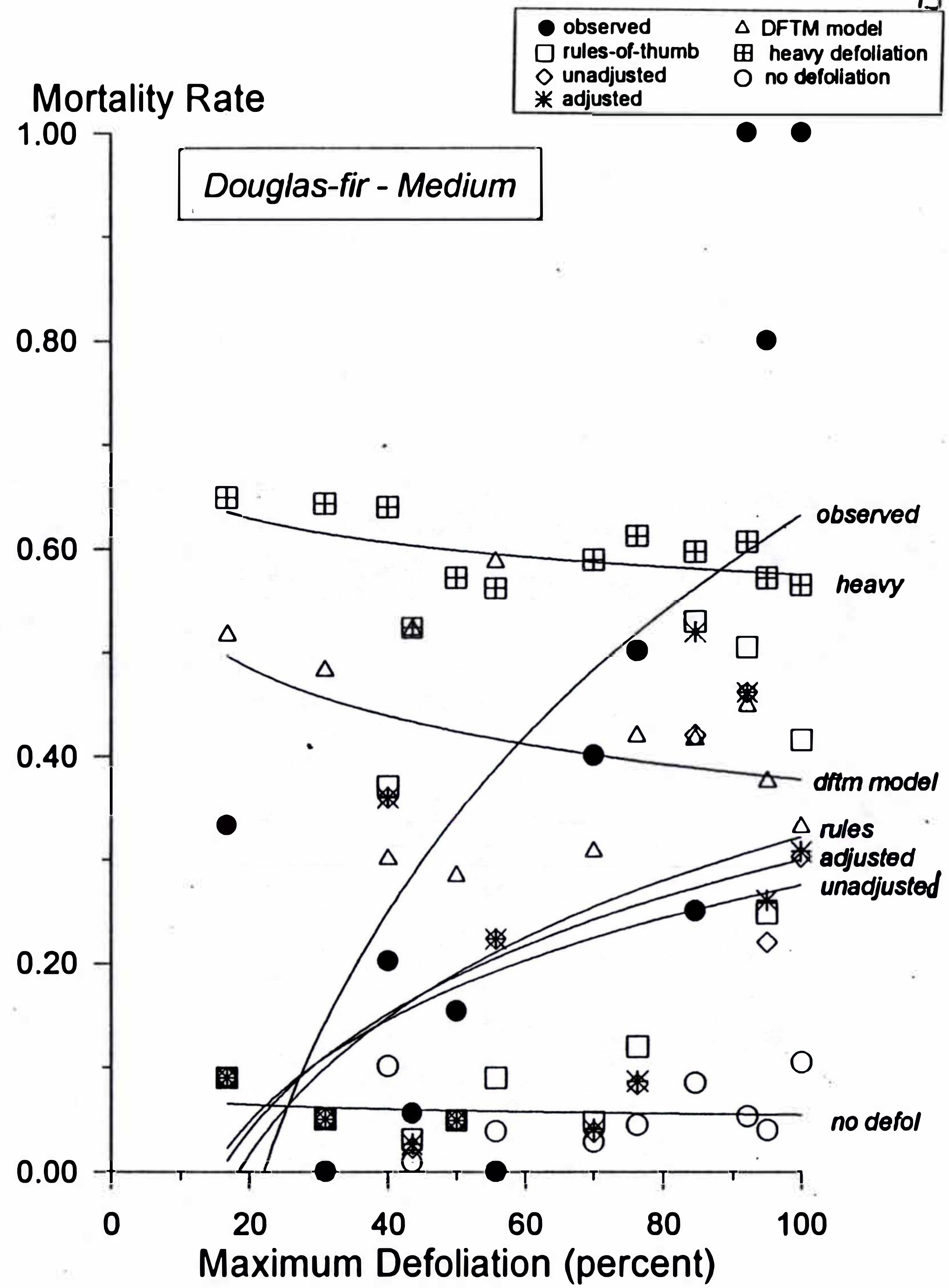

Figure 4 - Relation between mortality rate and defoliation for medium Douglas-firs.

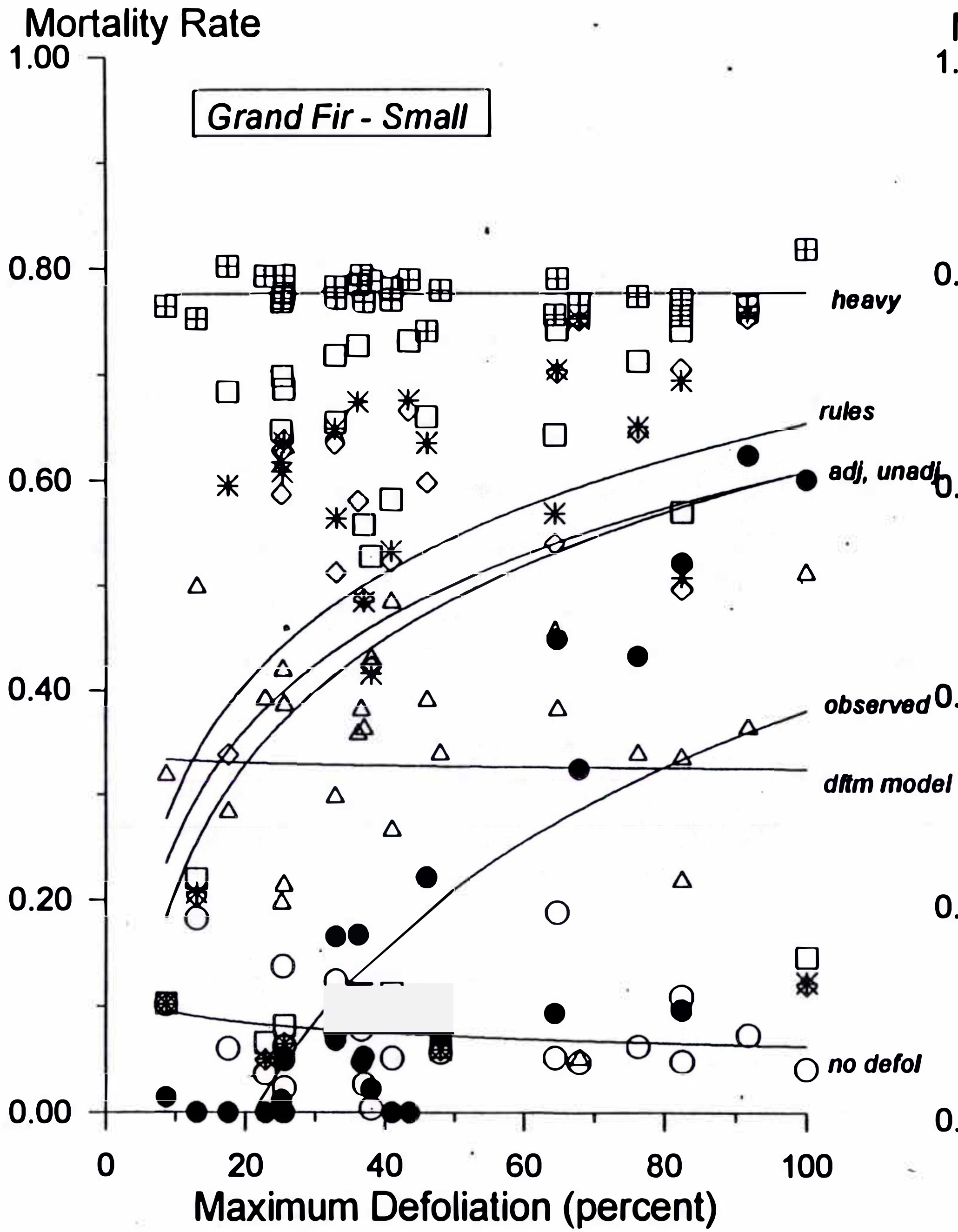

Figure 5 - Relation between mortality rate and defoliation for small grand firs.

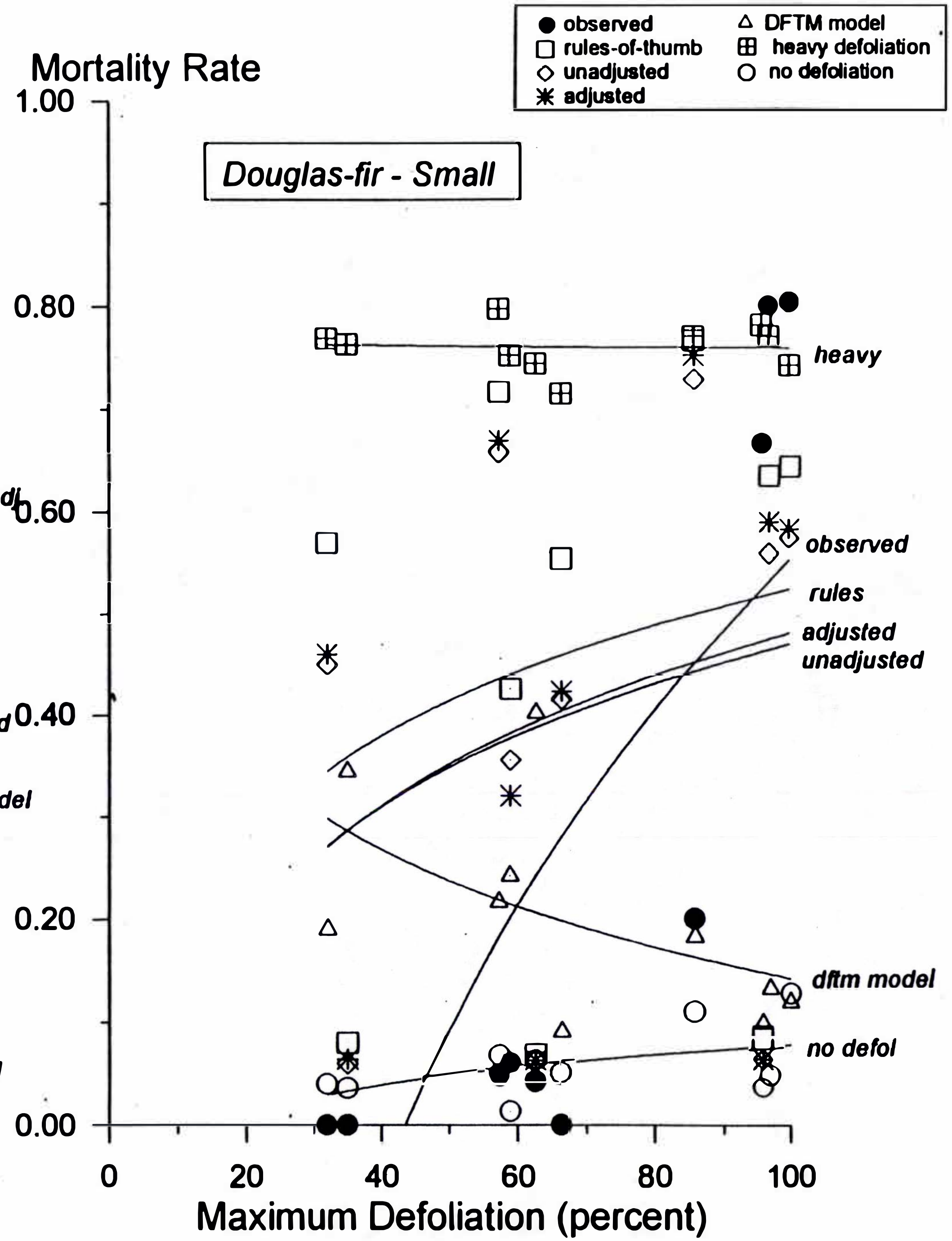

Figure 6 - Relation between mortality rate and defoliation for small Douglas-firs.

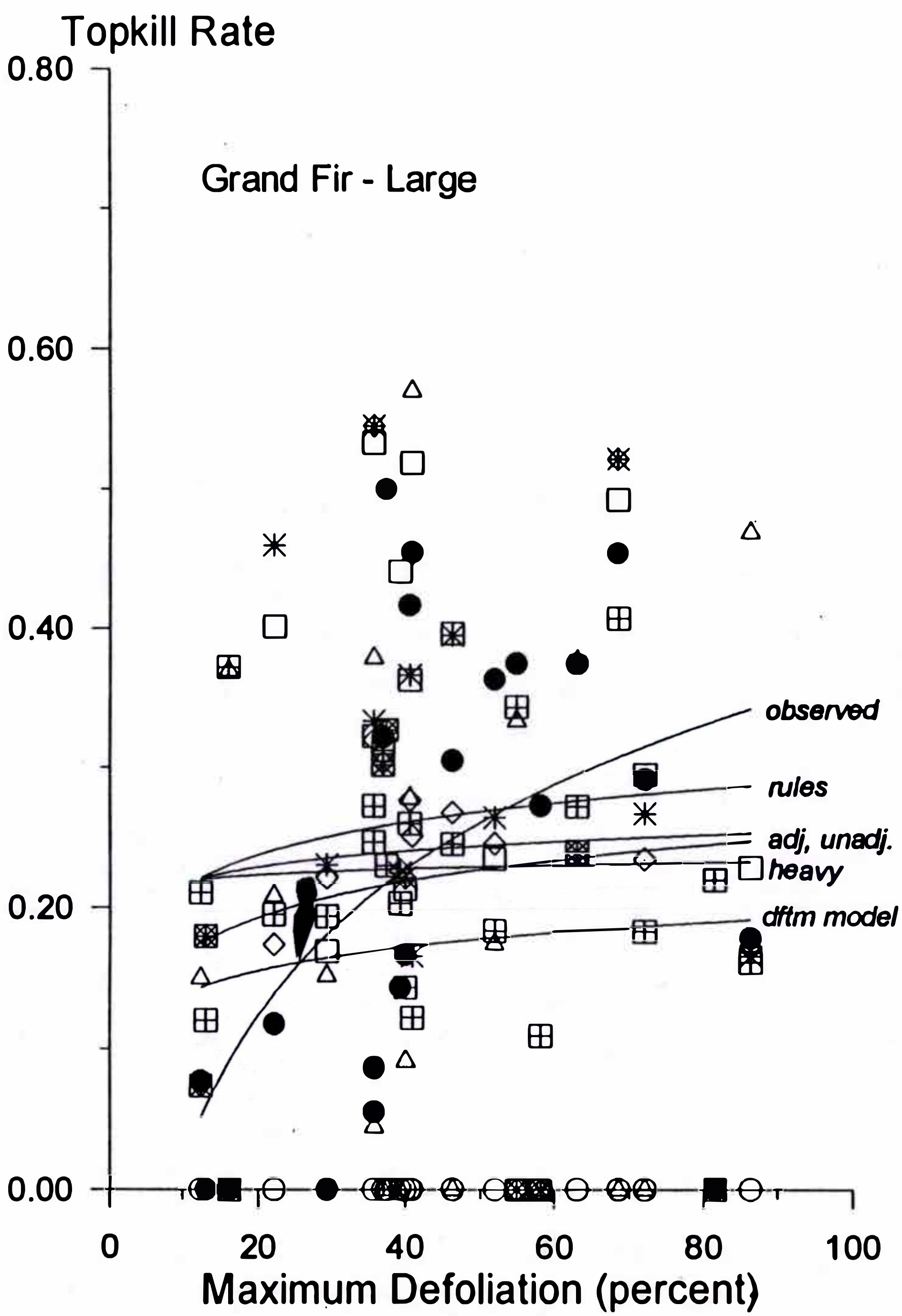

Figure 7 - Relation between topkill rate and defoliation for large grand firs.

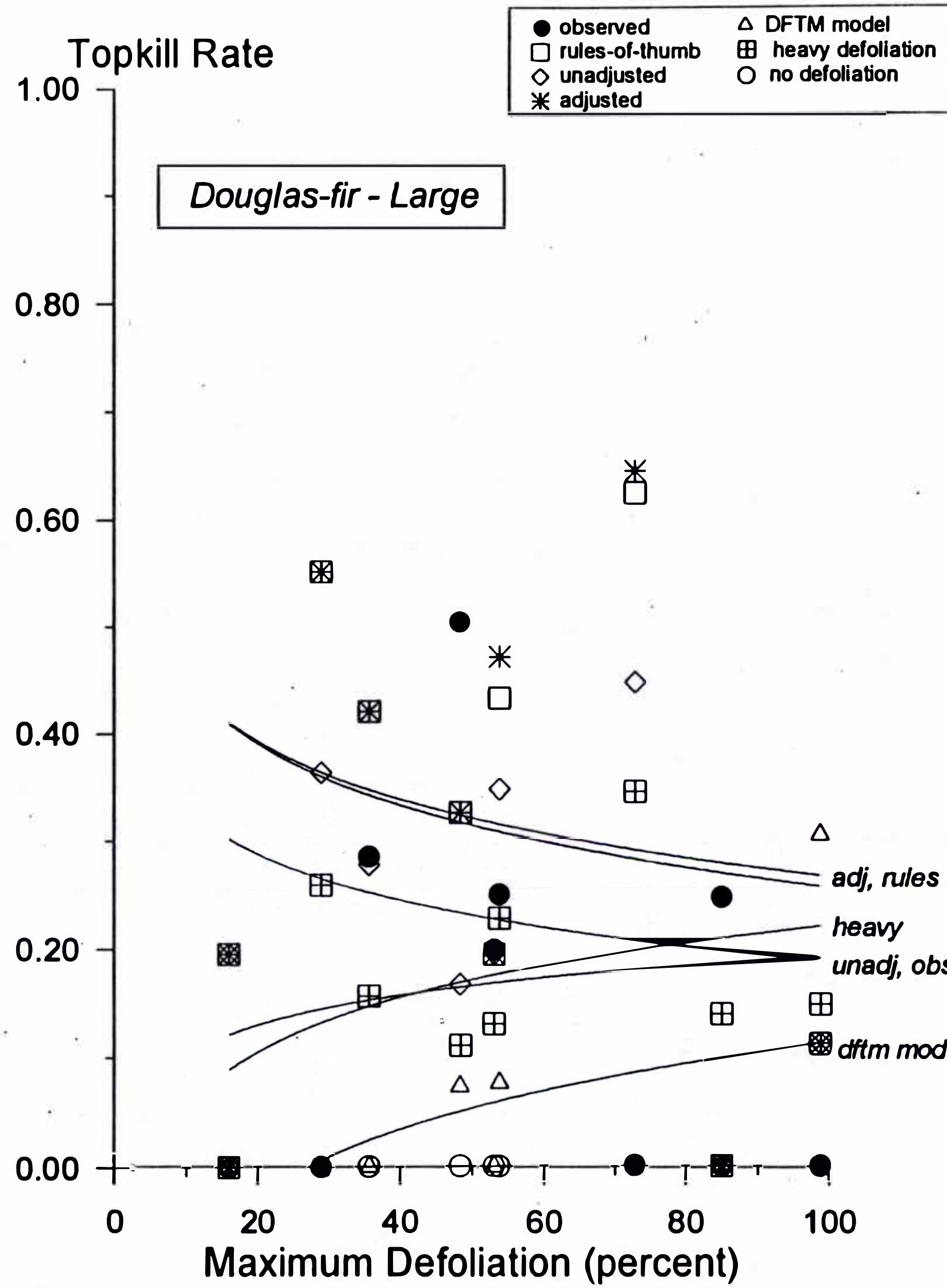

Figure 8 - Relation between topkill rate and defoliation for large Douglas-firs.

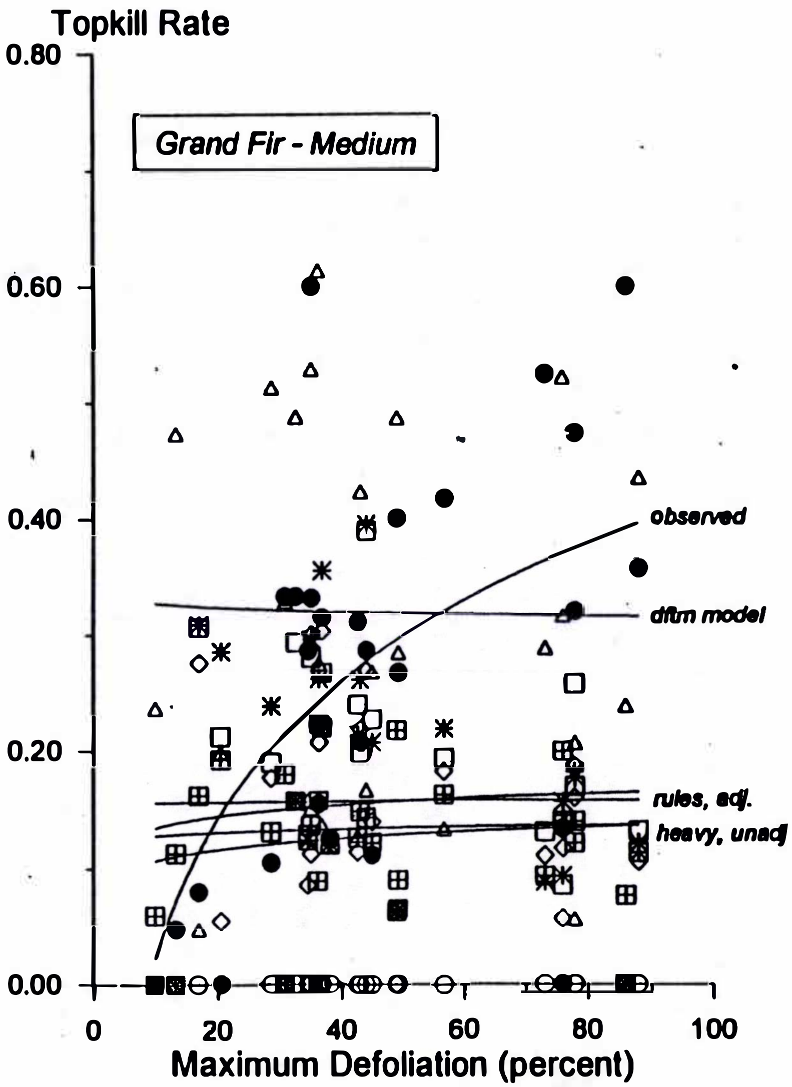

Figure 9 - Relation between topkill rate and defoliation for medium grand firs.

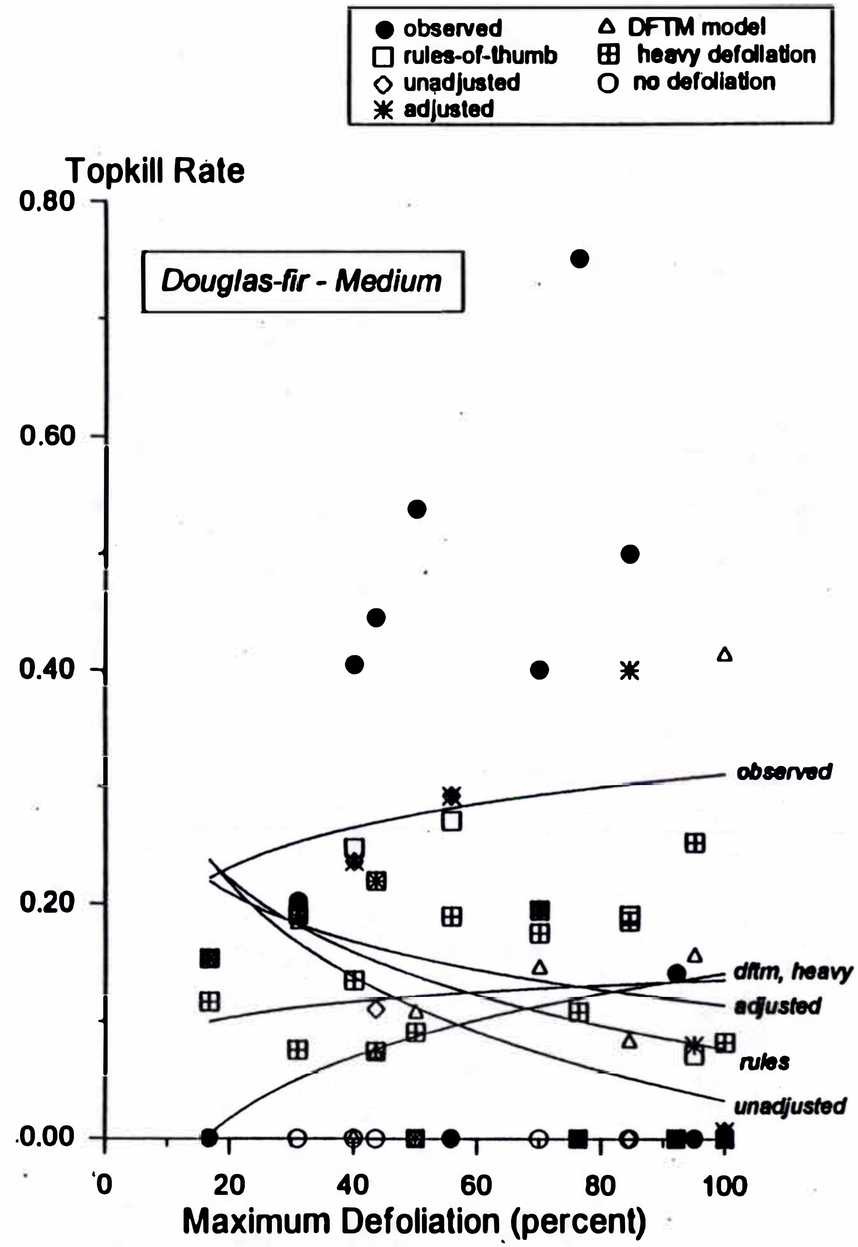

Figure 10 - Relation between topkill rate and defoliation for medium Douglas-firs.

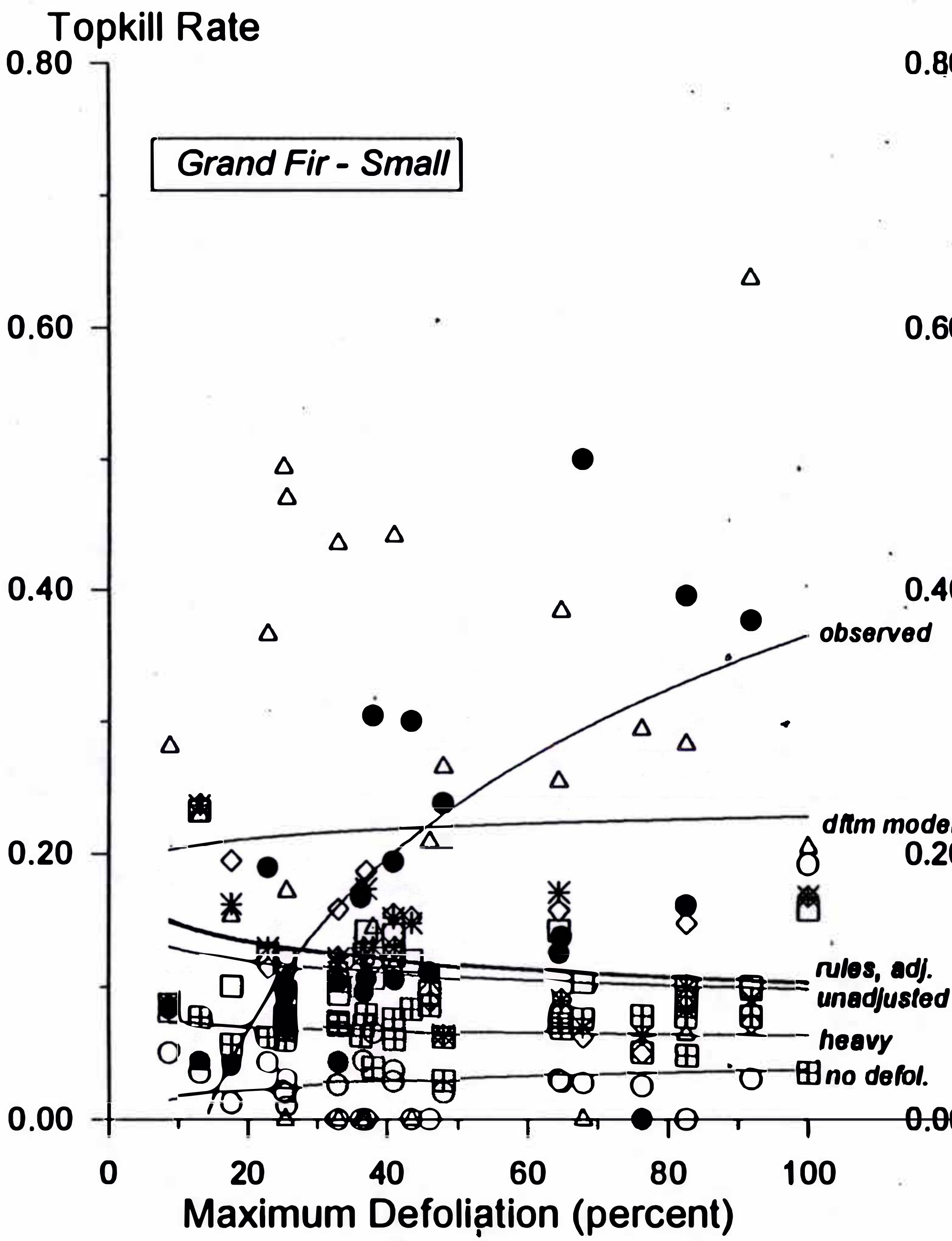

Figure 11 - Relation between topkill rate and defoliation for small grand firs.

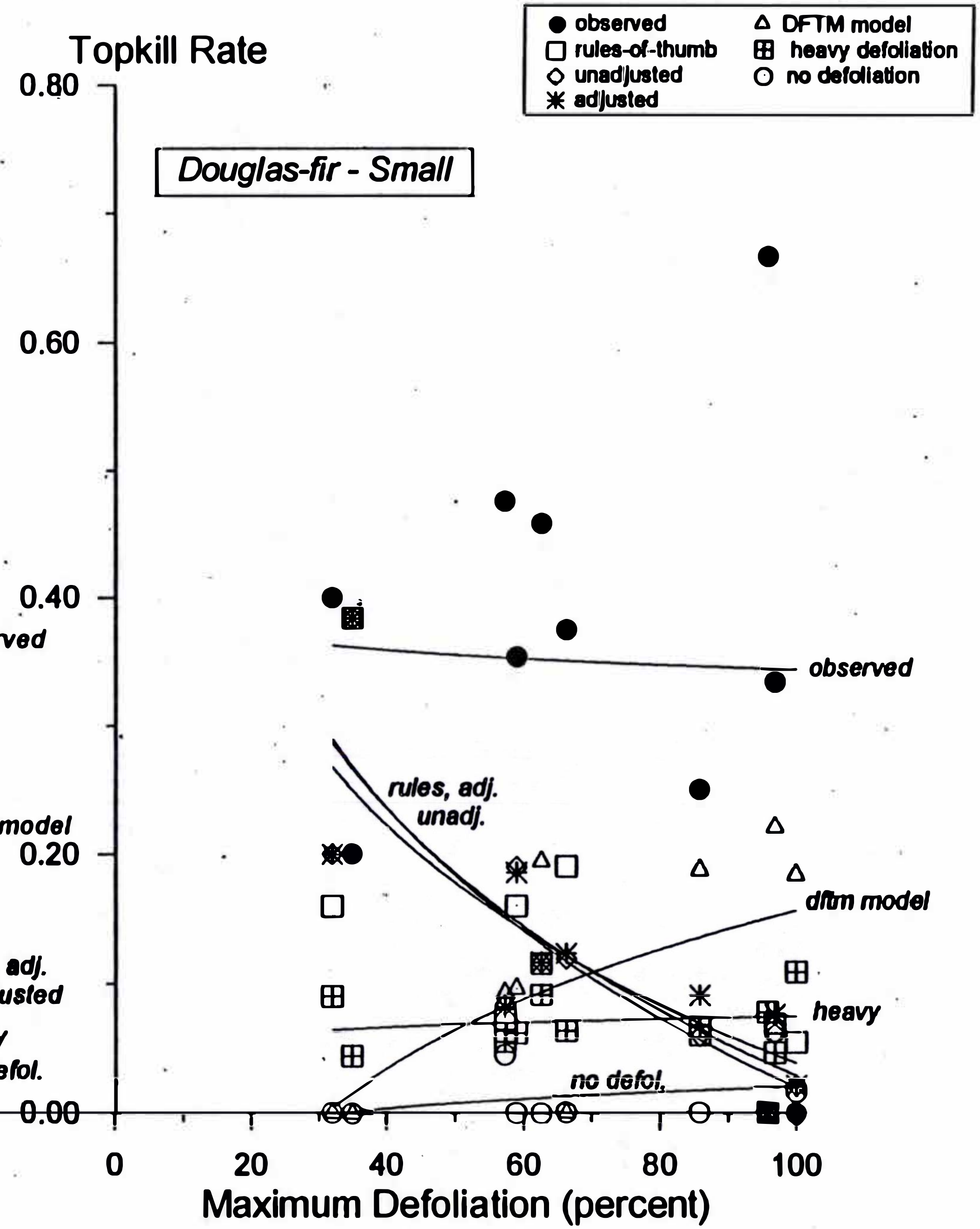

Figure 12 - Relation between topkill rate and defoliation for small Douglas-firs.

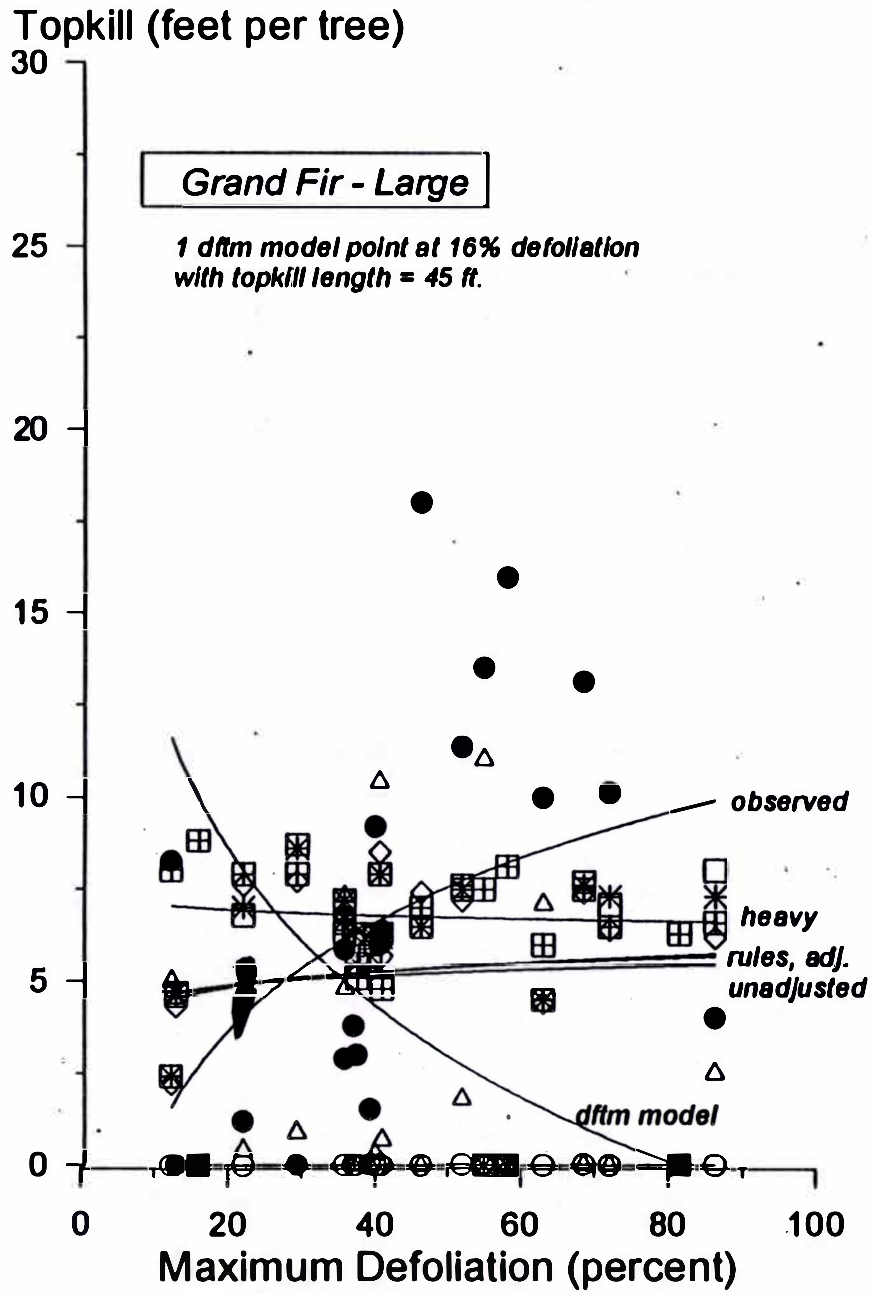

Figure 13 - Relation between topkill length and defoliation for large grand firs.

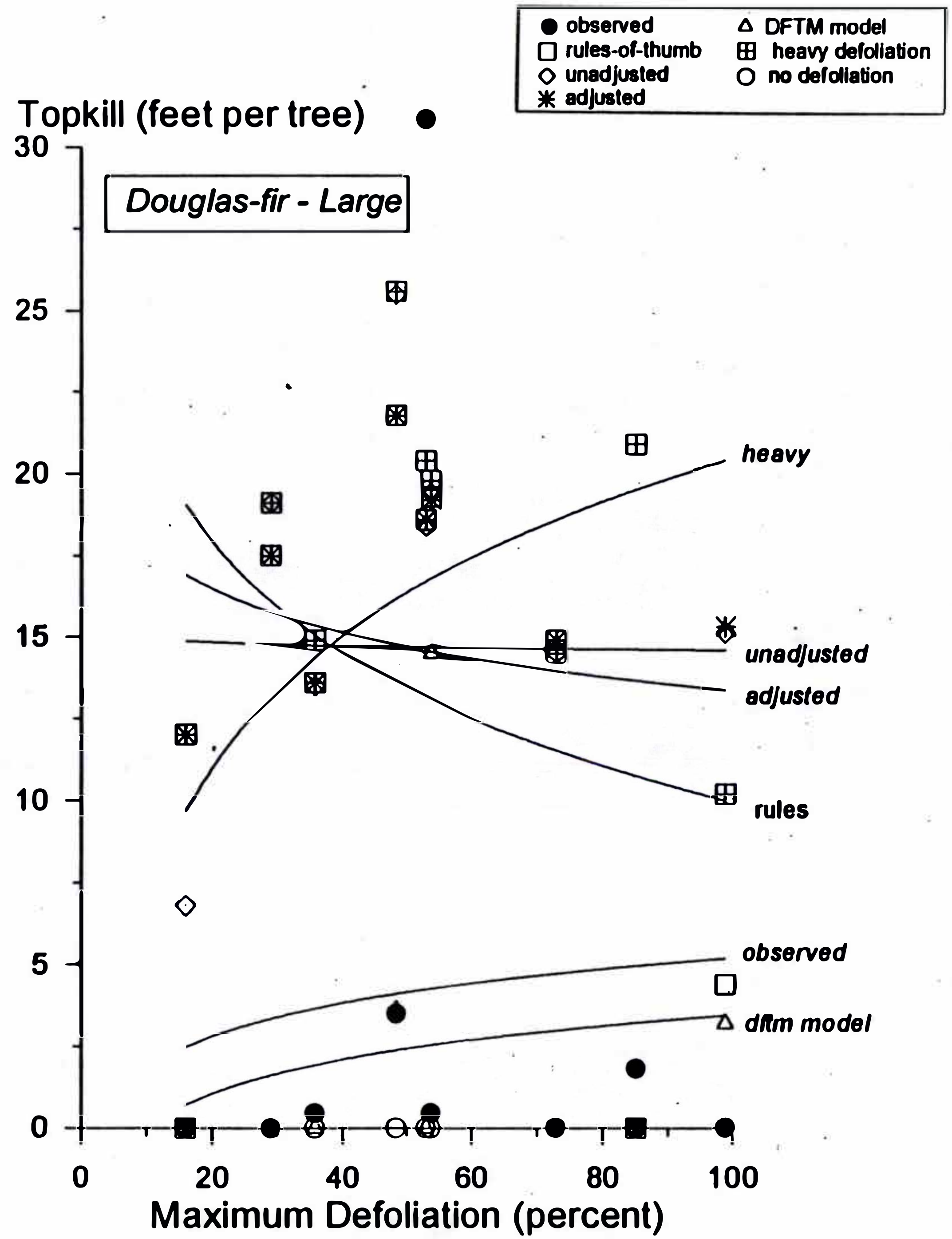

Figure 14 - Relation between topkill length and defoliation for large Douglas-firs.

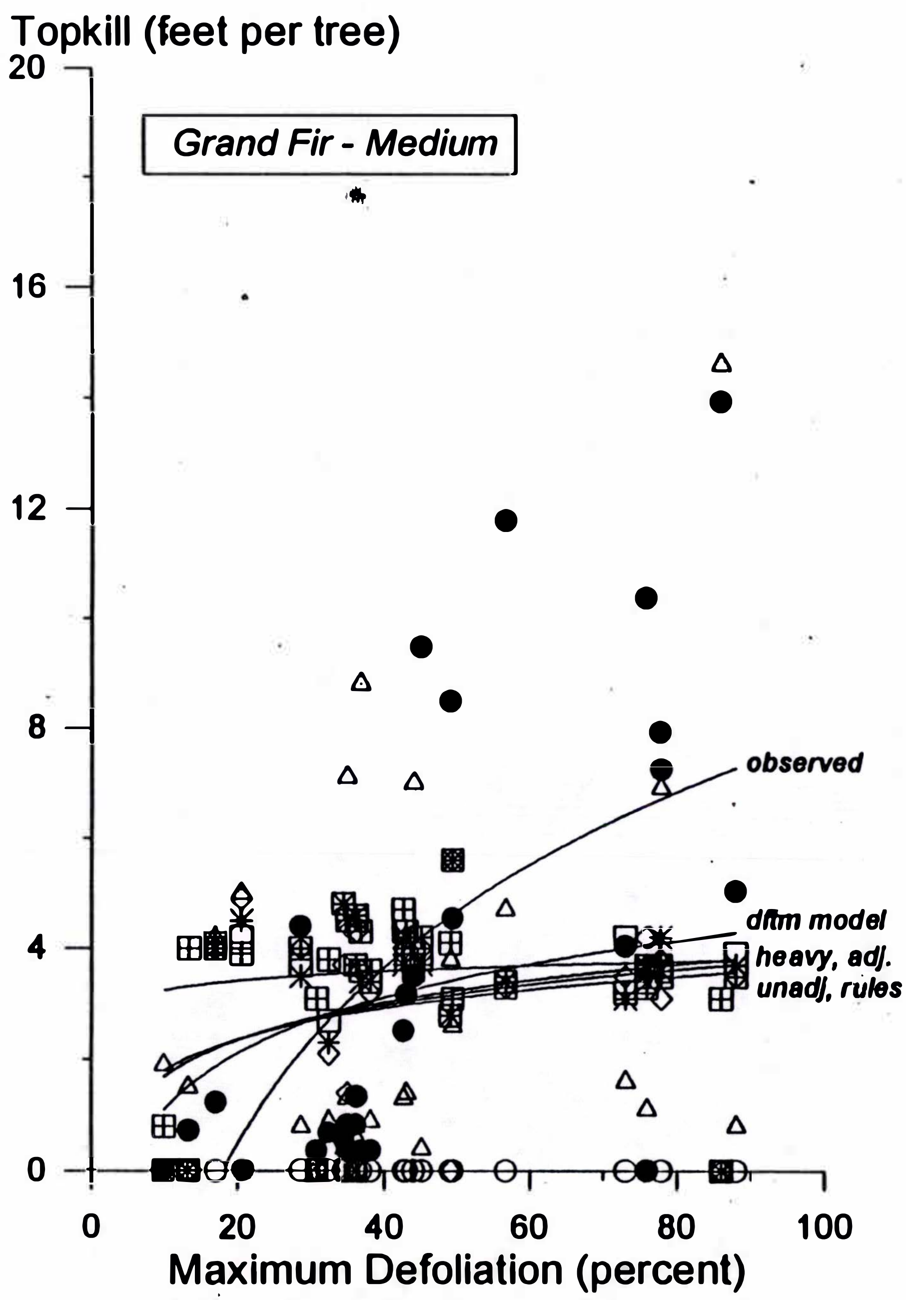

Figure 15 - Relation between topkill length and defoliation for medium grand firs.

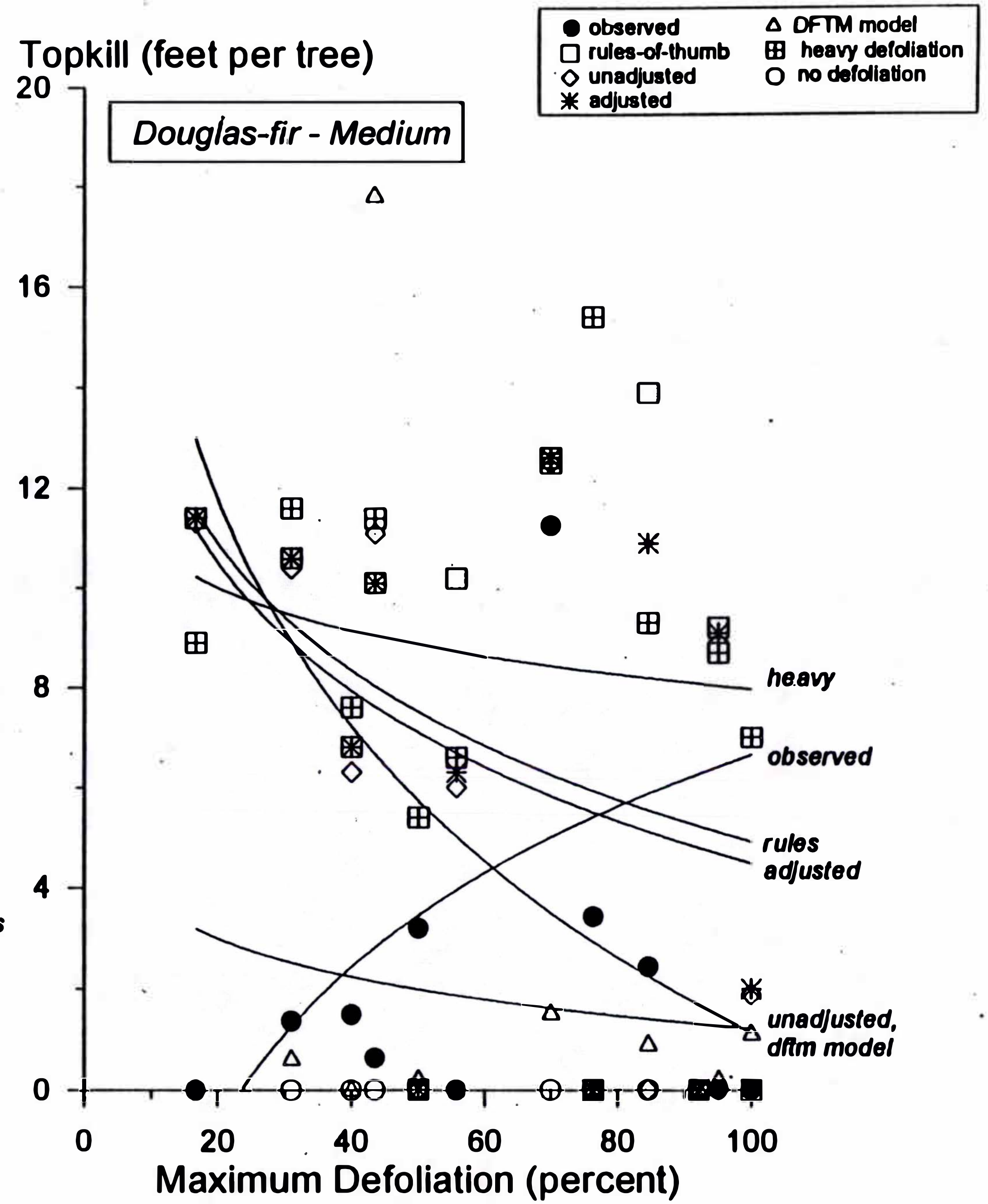

Figure 16 - Relation between topkill length and defoliatoin for medium Douglas-firs.

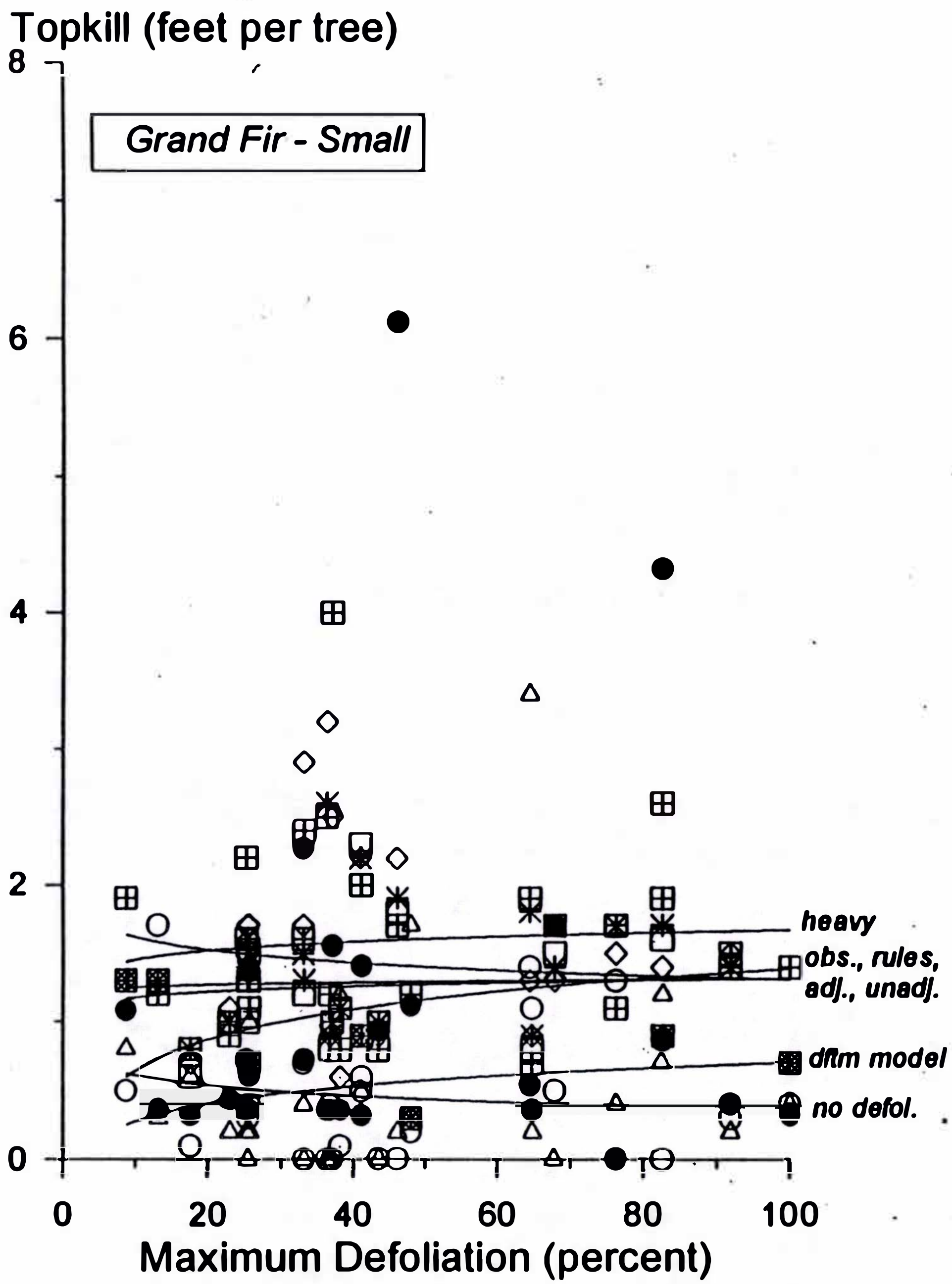

Figure 17 - Relation between topkill length and defoliation for small grand firs.

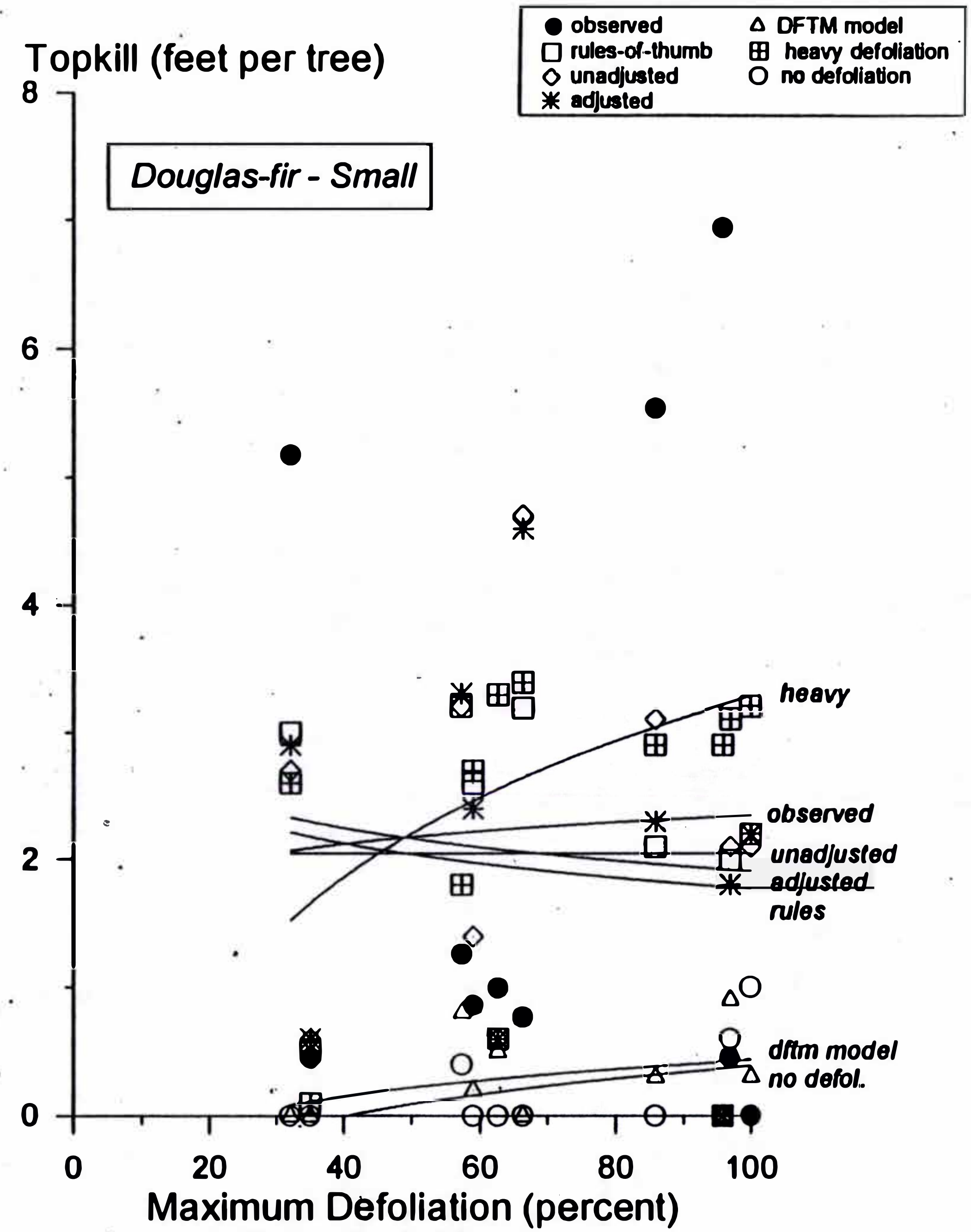

Figure 18 - Relation between topkill length and defoliation for small Douglas-firs.

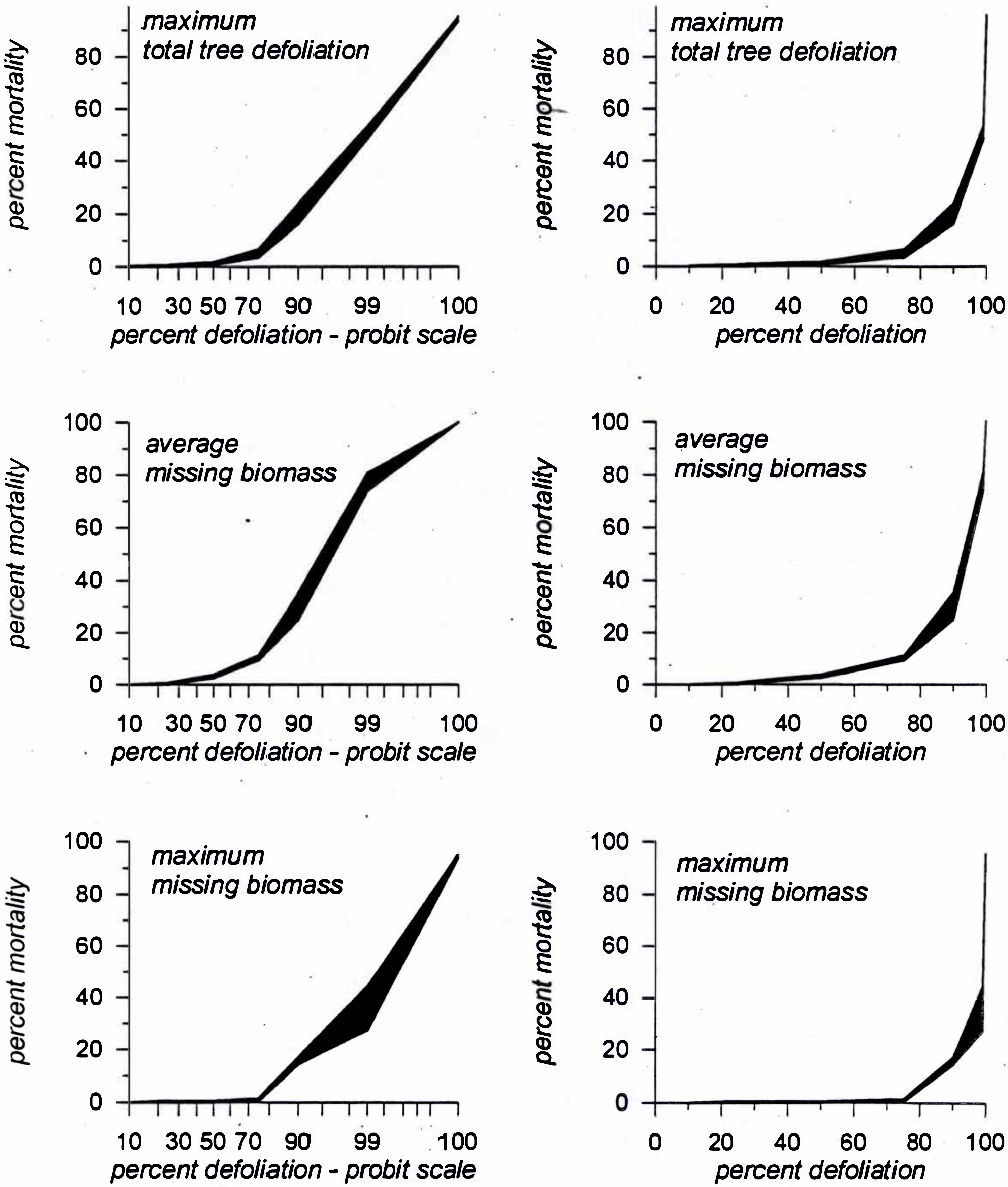

Figure 19. The relation between mortality caused by DFTM (unshaded) or bark beetles (shaded) and 3 different measures of defoliation (grand fir only, n=2245). For the x-axis, probit scales are used for the 3 graphs on the left, while linear scales are used for the 3 graphs on the right (modified from Wickman 1978, Fig. 7).

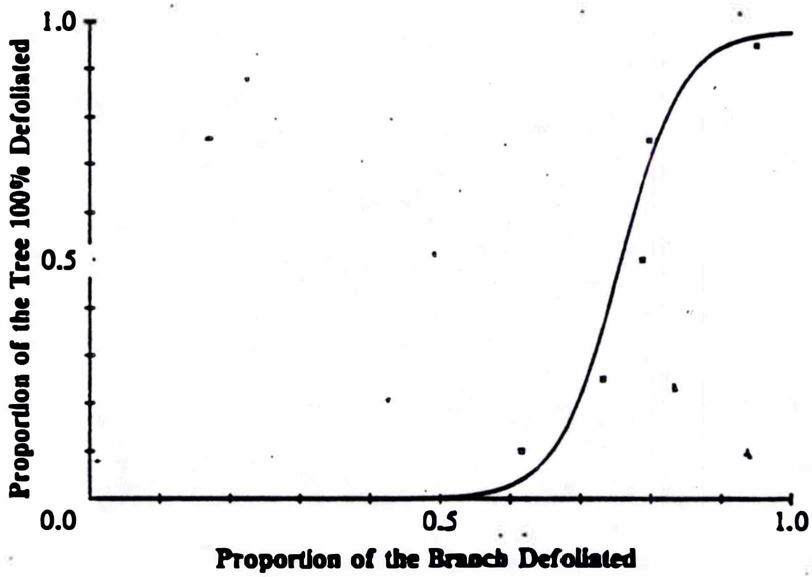

Figure 20. The relation between midcrown branch defoliation and proportion of the tree that is 100% defoliated (=whole tree defoliation) used in the Douglas-fir tussock moth Outbreak Model (taken from Overton and Colbert 1978, Fig. 4-38).

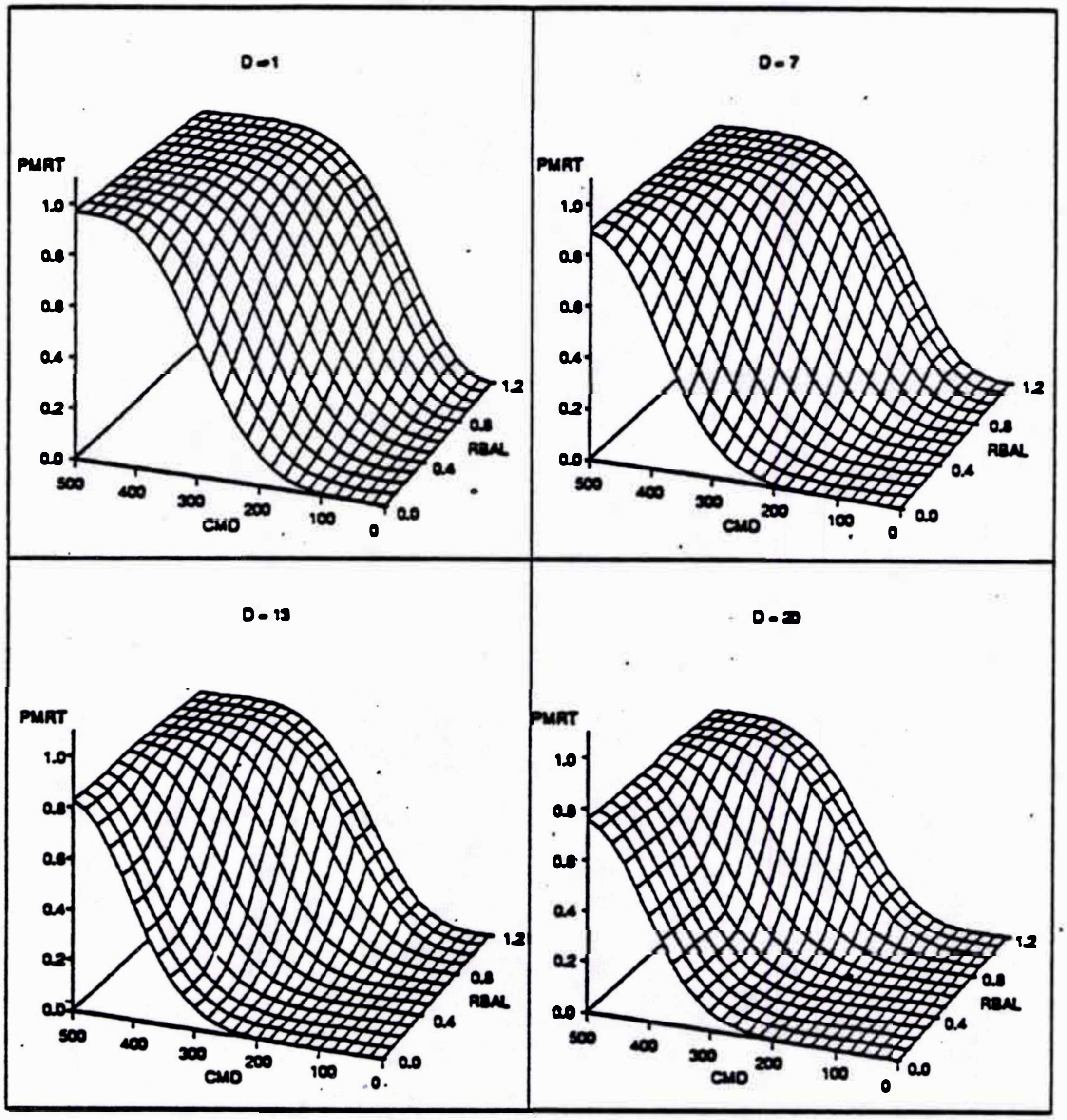

Figure 21. Relation between probability of tree mortality (PMRT), 5-year cumulative defoliation (CMD), and relative basal area in larger trees (RBAL) used in the WSB Damage Model, shown for different diameters (D) (taken from Crookston 1991, Fig. 19).

Appendix A

Description of IMPACT data

The data used for this analysis was collected by Boyd Wickman during the 1972-76 Douglas-fir tussock moth outbreak in the Blue Mountains (Wickman 1978, Wickman et al. 1980). Descriptions of the data items are shown below. When appropriate, a list of values for a data item is provided.

Data Item	*Description/contents*
subarea	*Geographical subarea code. Total number of subareas = 29, and the average number of plots per subarea = 11.8 (range = 5 to 28); when using FVS, we treated subareas as stands.*
plot	*Plot identification number. Total number of plots = 342, and the average number of trees per plot = 8.5 (range = 1 to 45); when using FVS, we treated plots as subsamples of a given stand (=subarea).*
defol	*Defoliation class code. Each subarea was given a defoliation class code (1= heavy, 2= moderate, 3= light, or 4= very light) by an on-the-ground observer.*
plot date	*Plot establishment date (month and year, starting with 8-72 and ending with 6-74).*
size	*Plot size in acres. All sample plots are .02 acres.*
tree	*Tree identification number.*
species	*Tree species code. Summary of sample trees:*

		Tree size class		
species	Total (# trees)	large (# trees)	medium (# trees)	small (# trees)
grand fir	2,245	375	579	1,291
Douglas-fir	433	81	146	206
western larch	114	30	60	24
Engelmann spruce	68	23	20	25
subalpine fir	28	4	11	13
lodgepole & ponderosa pine	22	5	7	10
other (unidentified)	8 9	---	---	---
total	2,918	518	823	1,569

dbh	*Diameter at breast height in inches. Range = 0.8 to 45.7*
volume	*Board foot volume, Scribner rule. Range = 59 to 3,129*

crown — Crown class (dominant, codominant, intermediate, or suppressed)

pdef1 — Total tree defoliation (percent) for year 1.
values present: 0 5 10 25 45 50 70 75 90 99 100

pdef2 — Total tree defoliation (percent) for year 2.
values present: 0 10 21 25 50 75 90 99 100

topkill — Topkill code. Summary of topkill observations:

code	description	observed no. of trees topkilled
1	leader only	252
2	0 - 10%	137
3	11 - 25%	43
4	26 - 50%	27
5	75%	83
6	old spike	61
7	broken top	115
8	old top damage with new leader	8
		726

cause — Cause-of-death code. Summary of observed causes of death:

	Cause	# trees killed
1	Douglas-fir tussock moth (Orgyia pseudotsugata)	395
2	fir engraver (Scolytus ventralis)	34
3	roundheaded fir borer (Tetropium abietis)	7
4	flatheaded fir borer (Melanophila drummondi)	0
5	S. ventralis and T. abietis or other combination	2
6	O. pseudotsugata and S. ventralis	0
7	other and unknown (windfall, fire, disease, etc.)	88
8	Douglas-fir beetle (Dendroctonus pseudotsugae)	14
9	logging	84
10	(meaning of this code is unknown)	4

year — Year of death. Summary of tree mortality by year:

Year	no. of trees killed
72	211
73	174
74	132
75	91
76	20

Notes on the processing of specific data items:

1. *Tree records were grouped by subarea, which resulted in 29 data sets that were processed as individual stands.*

2. *Defoliation class codes were summarized and used only for examination of the data, not as input for model simulations.*

3. *Since the number of plots that occurred within any subarea varied, the number of trees per acre represented by a single tree record also varied. Plots within a subarea were weighted equally when tree records were grouped into subareas.*

4. *Trees were assigned to one of three size classes (small, medium and large) based on species and dbh as described in Sheehan[1] and summarized below:*

species	size class	dbh range lower (in.)	dbh range upper (in.)
grand fir	small	---	5.7
	medium	5.8	11.3
	large	11.4	---
Douglas-fir	small	---	6.1
	medium	6.2	12.1
	large	12.2	---

5. *Total tree defoliation values were translated to missing biomass estimates as described in Sheehan et al. (1994). Separate equations were used for each species and size class.*

6. *Wickman (1978) reports topkill length by category (leader only, 0-10% of live crown, etc.). FVS, however, predicts the length of topkill in feet. For each tree, we converted the observed topkill category into estimates of length (feet) as follows.*

   We chose 5 subareas (basal area = 97 - 408 sq.ft./ac) and summarized the crown ratios predicted by FVS by species. These average crown ratios (grand fir: mean = .359, s.d.= .111; Douglas-fir: mean = .459, s.d.= .108) were used for all size classes. Next, for each tree we used diameter to calculate total tree height as described in Wykoff et al. (1982, p.51). We multiplied the total height by the average crown ratio to estimate the live crown length (in feet) for each tree. We then set the length of topkill equal to either 1 foot (topkill code 1), the midpoint of the observed range of the live crown (codes 2, 3, and 4), or 75% of the live crown (code 5). Topkill codes 6, 7, and 8 were ignored because they reported topkill that had occurred prior to defoliation by DFTM.

7. *Output from the FVS model does not separate tree mortality by cause of death; previous analyses of the observed data, however, had examined the effects of defoliation on mortality caused by DFTM and by bark beetles. We therefore summarized observed tree mortality for all causes of death and for DFTM and bark beetles.*